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Palaeoecologic aspects of an Ordovician *Tretaspis* fauna

ABSTRACT: Different isocommunity lineages with successive metacommunities constitute the *Tretaspis* fauna of central, north, and west Europe. The fauna is strongly dominated by trilobites. Based on collections from one fossiliferous level in one locality a trial is made to grasp the autecology of some trilobite constituents. Most trilobites in the fauna were obviously benthic. Odontopleurids and *Tretaspis* show adaptations for a life on a flat surface and the latter probably burrowed shallowly. The food may have consisted of soft-skinned animals. *Panderia* may have burrowed backwards to form a dwelling burrow. *Remopleurides* and *Cyclopyge* have large eyes and large space for appendage muscles and were probably agile hunters, nekto-benthic or possibly pelagic. The excessive development of alimentary caeca in agnostids is a character shared with extant arthropods feeding on fluids, and in combination with the flattened shape this indicates that agnostids, including *Trinodus*, were ectoparasitic. The sea is judged to have been about 100 m deep.

INTRODUCTION

While the hard-skeleton morphology of trilobites is comparatively well known from many thousands of species, other aspects of this arthropod group have been difficult to treat because of the lack of pertinent information. Only regarding the construction of the appendages and the digging activity, as revealed by trace fossils, do we have some additional information, and the X-ray technique has barely begun to reveal details of the anatomy. The mode of life and way of feeding as well as the structure of trilobite communities can not be directly observed and it is therefore still more difficult to form a reliable opinion of these activities and

conditions. However, the author believes that there are some possibilities to draw conclusions from the coupling of certain morphological characters with environmental factors.

The aim of this contribution is to grasp the ecology of a *Tretaspis* fauna. For convenience and objectivity, the treatment is based on a collection from a limited horizon in a single quarry.

THE *TRETASPIS* FAUNA AND COMMUNITIES

Tretaspis and a number of associated genera characterize a belt of Lower and Middle Ashgillian (Upper Ordovician) rocks extending from Jämtland in Scandinavian to Czechoslovakia through Poland. Similar associations are found in the British Isles. The *Tretaspis* fauna of the whole of this area is by no means uniform, but should probably be split into separate communities and community lineages. For instance, a Bohemian type, characterized by the brachiopod *Foliomena folium* (Barrande) is present in Czechoslovakia and in Scania, while a community lineage with small brachiopods of non-Bohemian type is characteristic of Västergötland. The latter lineage may be split into an early community with *Tretaspis seticornis* and a succeeding community with *Tretaspis latilimba*. The communities within an evolving lineage may be distinguished as *metacommunities*, while the similar contemporaneous communities may be termed *isocommunities*. The *Tretaspis* fauna therefore consists of an array of iso- and metacommunities dominated by trilobites, of which cheiruraceans and trinucleaceans, notably *Tretaspis*, make up an important part.

LOCALITY AND HORIZON

The fauna in the following text was collected in a now abandoned quarry at Skultorp, on the eastern slope of southern Mt Billingen, in Västergötland, south-central Sweden. The position in the grid map was given by Bergström (1968b, p. 4, locality no. 18) as VE 308684 in the topographical map (Topografisk karta över Sverige, on 1 : 50 000). A detailed account of the succession exposed below the intruded carbonatic, yellowish-green sill, which separates the *Tretaspis* Mudstones from the Dalmanitina Beds, and in a core continuing down into the Middle Ordovician Dalby Limestone, was given by Skoglund (1963, pp. 13—15). The uppermost 12.5 m of this sequence consist mainly of greyish mudstones, constituting the Ulunda Mudstone of Jaanusson (1963). The fossiliferous band is situated about 2.7—3.0 m below the above-mentioned sill and consists of light-coloured siltstone and speckled mudstone (Fig. 1). The fossils have mostly been collected in loose boulders because of inaccessibility of the vertical outcrop, and the exact thickness of the fossiliferous horizon

is thus not known. Most of the specimens, but not all of them, are preserved in the light-coloured siltstone. Contrary to the conditions in the fossiliferous speckled mudstone, the siltstone does not show any signs of biogenic reworking.

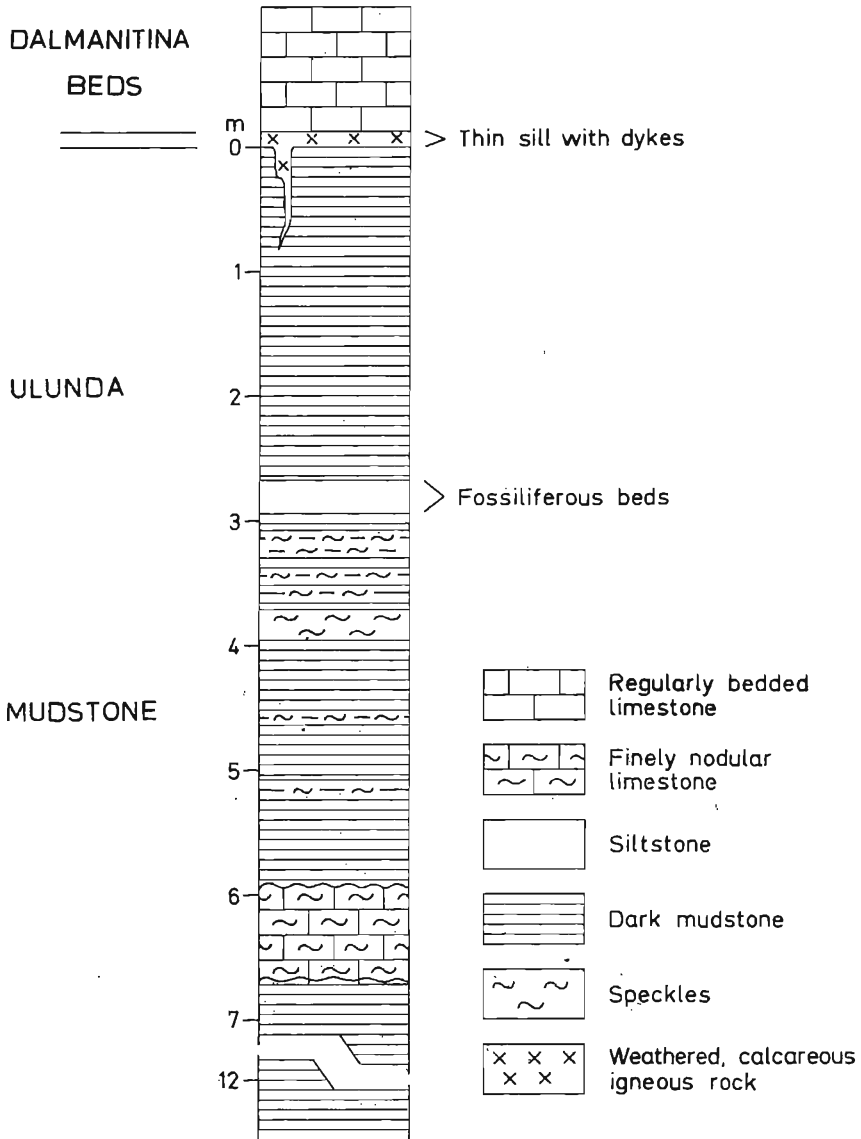


Fig. 1

Schematic drawing of the Skultorp section through Upper Ordovician rocks; the Ulunda Mudstone forms the top of the *Tretaspis* mudstones
 The drawings in this paper are made by Mrs Siri Bergström

PREMISES FOR THE TREATMENT

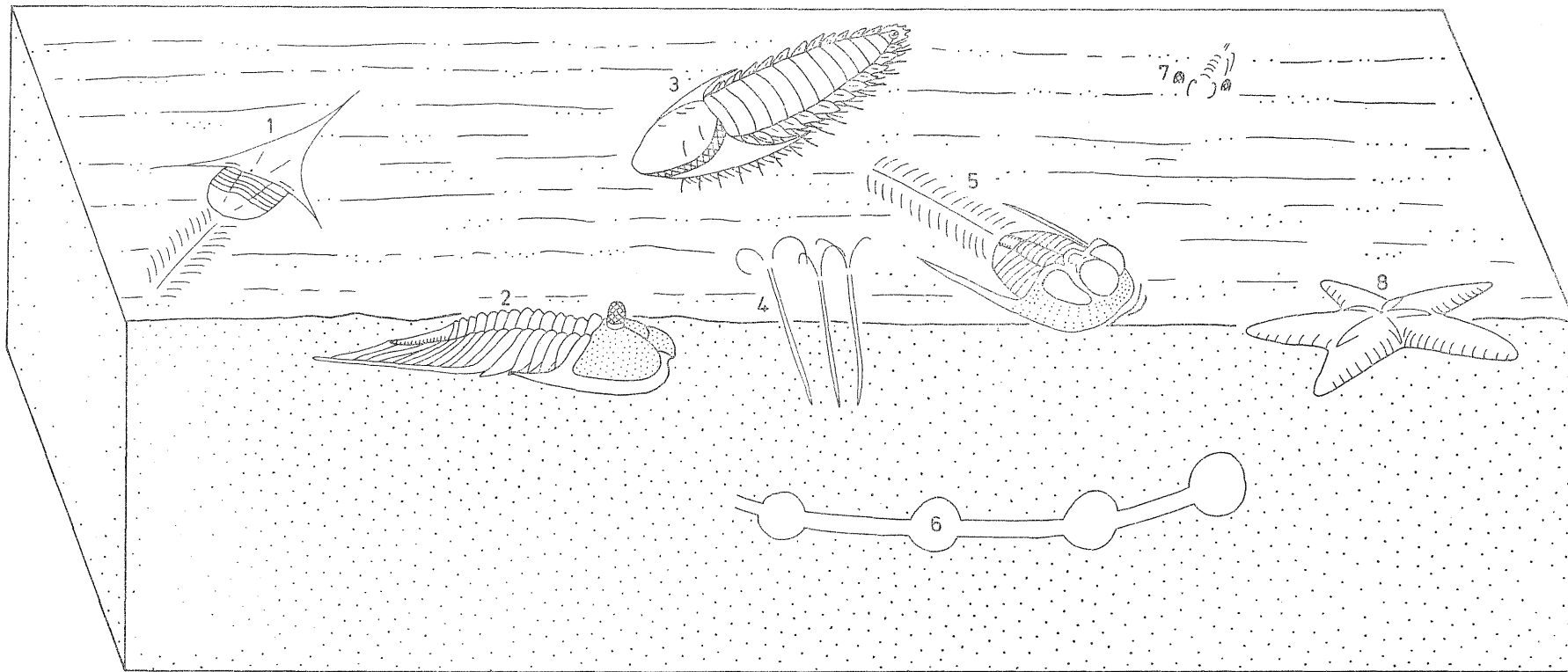
In the discussion of the particular palaeoecological aspects on the Skultorp fauna, the actual material collected at Skultorp is commonly insufficient. In many cases the morphology is better known from other material of the same species than those occurring at Skultorp, although in some cases, notably *Hadromeros subulatus*, the most complete material known was collected at Skultorp. Regarding other specific features such as distribution in different types of facies, it is obviously also necessary to extend the discussion outside the Skultorp quarry.

In some cases, valuable indications can be obtained from a comparison with related or even unrelated trilobites in which a particular feature is well understood. In the discussion of the function of the appendages, which is closely related to the question of feeding manners, valuable information can be obtained from the study of trilobite trails, although those trails discussed certainly were not produced by any of the species particularly concerned in this paper.

Furthermore, a comparison with extant crustaceans and particularly their mode of life and specializations analogous to those found in trilobites may be revealing, as the living animals allow us to study the interdependence between morphology and habits. The probably fairly large phylogenetic distance between crustaceans and trilobites is in accord with a great discrepancy in many morphologic details. On the other hand, this common dissimilarity may make a casual close correspondance in morphology more trustworthy as an indication of functional similarity.

The general working model delineated above is not without fallacies. It is not always sure that closely related species found in different habitats are characterized by similar habits. In his study of the modern American soft bottom *Nephtys incisa* — *Nucula proxima* community, Sanders (1960, pp. 148—150) found that a number of polychaetes, belonging to groups which are typically carnivorous, feed on detritus in this particular case. Indeed, not even when very similar species live side by side is it safe to conclude that their mode of living is similar. This may be exemplified by ophiurids in the eastern North Atlantic epifaunal *Modiola modiolus* community (cf. Thorson 1968, pp. 212—213). *Ophiothrix fragilis* is mostly found on the coral *Alcyonium digitatum* or on poriferans, where it feeds by filtering, taking advantage of the current produced by the other animal. The similar *Ophiocomina nigra* may also feed from plankton, but is dominantly carnivorous. *Ophiopholis aculeata* is intermediate in food habits, but differs in being specialized to creep into very narrow cavities and crevices. These differences would hardly be suspected from a study the morphology or general environment only.

Although it is thus nearly impossible to get a truly reliable result in any specific case, it appears probable that at least some general ecologic aspects of the treated fauna may come out fairly well.



Life in the *Tretaspis* sea at Skultorp

1 — *Lonchodomas portlocki*, 2 and 7 — *Cybeloides loveni*, 3 — *Remopleurides* sp., 4 — animals represented by probable dwelling tubes, 5 — *Tretaspis latilimba*, 6 — trace fossil resembling *Hormosiroidea*, 8 — asterozoan

THE FAUNA AT SKULTORP

The fauna is a typical *Tretaspis* fauna, dominated by trilobites (cf. Pls 1—2), several species of which belong in the Trinucleacea and Cheiruracea. In addition to the trilobites, there are a few brachiopods, ostracodes, a single asteroid, and "worm" tubes. In the author's opinion, the composition of the fauna as expressed in certain high taxa may tell a great deal

Table 1

List of trilobites in the *Tretaspis* fauna of the Ulunda Mudstone at Skultorp, Västergötland, Sweden

TRILOBITA	Total	Articu- lated	Enrolled	Upper Jonstorp Mudstone	Älleberg Beds
Geragnostidae					
<u>Trinodus tardus</u>	11	1	1	+	+
Trinucleidae					
<u>Tretaspis latilimba</u>	29	7	3	+	
<u>Tretaspis granulata</u>	2			+	+
Dionididae					
<u>Dionide cf. euglypta</u>	1			+	
Raphiophoridae					
<u>Lonchodomas portlocki</u>	12	7		+	
Homalonotidae					
<u>Brongniartella cf. platynota</u>	1				
Cheiruridae					
<u>Hadromeros subulatus</u>	5	2		+	
<u>Skelipyx sp.</u>	2	1			
<u>Pseudosphaerexochus sp.</u>	3				
<u>Sphaerocoryphe dentata</u>	1	1		+	
Enorinuridae					
<u>Cybeloides loveni</u>	13	5		+	
Odontopleuridae					
<u>Diacanthaspis ceccoantha</u>	1			+	
<u>Primaspis sp.</u>	1				
Lichidae					
<u>Platylidas laxatus</u>	2	1		+	
Remopleurididae					
<u>Remopleurides sp.</u>	10	5	2	+	?
Cyclopygidae					
<u>Cyclopyge sp.</u>	1	1	1		
Proetidae					
<u>Decoroproetus sp.</u>	1	1			
Illaeidae					
<u>"Illaeus" angelini</u>	5	2		+	
<u>"Illaeus" cf. angelini</u>	2				
<u>Panderia megalophthalma</u>	1			+	+
Dalmanitidae					
<u>Zeliskella? sp.</u>	2	2	1		
Total:	106	36	8	13	3

about the type of fauna and the taxa in question are therefore given in the list of species and specimens (Tables 1—2).

As is generally the case in the reddish-brown or greenish *Tretaspis* mudstones (Jonstorp Formation), the fauna is mostly confined to a fairly thin fossiliferous horizon which wedges out laterally. No such horizon was previously known from the Ulunda Mudstone below the Alleberg Beds, and the fauna reported is consequently the first rich fauna found in these strata. A few isolated trilobite finds were summarized by Jaanusson (1963, p. 123). From poorly fossiliferous beds at several localities peculiar endichnial structures are also known, reminiscent of a string of pearls and possibly referable to *Hormosiroidea*? Although studied by Dr. Roland Skoglund, these structures have not been reported in the literature. It may be remarked that at Allebergsände, where the Ulunda Mudstone is only a few metres thick, the endichnial structures have apparently only been found in the upper part of the Jonstorp Formation.

As seen in Table 1, there is a high degree of more or less conjoined trilobite specimens. This fact is remarkable but not exceptional, as similar conditions are met with in other fossiliferous bands in the *Tretaspis* mudstones as well. Several specimens were found enrolled or with intact sutures indicating that they were embedded as dead individuals rather than as moult exuviae. This fact, the unrestricted size distribution and the presence of an intact arm of an asterozoan clearly indicates that the Skultorp fauna was buried close to the place where it lived.

It was shown on modern bottom faunas from the Gulf of Mexico by Odum, Cantlon & Cornicker (1960) that there is a fairly regular relationship between the cumulative number of species encountered and the number of individuals counted. This observation makes possible a comparison between the diversity of different faunas, even when the number of known specimens is not of comparable orders. For easy comparison the use of a diversity index is useful. On fossil material a diversity index was first used for comparison by Ziegler, Cocks & Bambach (1968), who used the following relationship:

$$\left[\text{Diversity index} = \frac{\text{Number of species}}{\text{Log of the number of individuals}} \right]$$

It is not evident from the text that these authors rely on the result of Odum & *al.* but this is probably the case. In applying this method to the material, Ziegler & *al.* reduced the counts to comparable entities by using the number of the most abundant valve in two-valved organisms and by dividing the number of trilobite remains (the most abundant part of the exoskeleton) by 10 to allow for ecdysis (following an estimation by Harrington 1959). Infrequent crinoid ossicles were counted as 1.

In detail, this procedure is not applicable in the present case. The reason for this has been hinted at above: the trilobite remains are to a large extent the remains of dead individuals, not of exuviae. The author has chosen to divide the trilobite number only by 2. In consequence, the number of ostracodes have been divided by 4. With these modifications, the diversity index of the present fauna is 16.6. Without the modifications, the diversity index would be 14.3.

There is a striking similarity between the present fauna and that known from the Upper Jonstorp Mudstone (Red Tretaspis Shale). In fact, all the trilobites determined to species level except *Brongniartella* cf. *platynota* have been found previously in the Upper Jonstorp Mudstone. *B. platynota* is known only from the *Dalmanitina* Beds. This circumstance strongly supports the opinion (Jaanusson 1963, p. 118) that the main part of the Ulunda Mudstone is a regional colour variant of the Upper Jonstorp Mudstone.

As noted above, the fauna may be regarded as a typical *Tretaspis* fauna. As such it is characterized by a dominance of trilobites (Fig. 2). The most distinctive trilobite groups in the *Tretaspis* fauna are considered to be Remopleurididae, Cyclopygidae, Illaenacea, Cheiruracea, Odontopleuridae, Trinucleacea, and Agnostina. A number of species are listed by Kielan (1959, p. 22) as especially widespread: *Amphitryon radians*, *Cyclopyge speciosa*, *Dindymene ornata*, *Phillipsinella parabola*, *Tretaspis*

Table 2

Number of non-trilobite fossils in the *Tretaspis* fauna of the Ulunda Mudstone at Skultorp, Västergötland. The list includes finds from the fossiliferous horizon. Outside this horizon only *Hormosiroidea*-like trace fossils have been found in this section

CRUSTACEA:	
Ostracoda	
sigmoopsids	7
smooth ostracods	2
BRACHIOPODA:	
Orthacea	
<u>Skenidioides?</u> sp.	12
Plectambonitacea	
<u>Bimuria</u> sp.	5
sowerbyellid	1
plectambonitacean sp. 1	5
plectambonitacean sp. 2	2
Athyridacea	
smooth athyridaceans	2
ECHINODERMATA:	
asterozoan	1
TRACE FOSSILS:	
tubes	5

granulata, *T. seticornis*, and *Trinodus tardus*. The *Tretaspis* fauna lived during Early and Middle Ashgill times. In this time interval it was subject to evolutionary and other changes, making the early and late faunal aspects slightly different from one another. Yet as a whole the fauna is readily distinguishable, many constituents being virtually constant as well as the mudstone facies.

ASPECTS ON THE AGNOSTID *TRINODUS*

Regarding *Trinodus tardus* as well as other agnostids there is comparatively little evidence bearing directly on its mode of living and feeding. The unique combination of characters typical for agnostids makes it impossible to make a close comparison with any other trilobites.

Dr. Jaanusson pointed out for the author that agnostids are commonly comparatively widespread (cf. Whittington 1966, p. 728; Fig. 15) and that this distributional feature has been taken as an indication that agnostids were planktic. Faunistic features have also been taken as evidence for a planktic existence for some agnostids (Öpik 1961).

A wide distribution in itself is not evidence for a planktic existence, but rather indicates that feasible living conditions for the species in question prevailed over large areas. In modern seas this would indicate either a pelagic or a soft-bottom habitat (only exceptionally hard bottoms prevail over large areas). These two habitat types differ from each other in their distribution mechanisms, as distribution by means of eggs and larvae is much more important in the latter than in the former. This difference is very difficult to recognize in fossil faunas, however. Another difference is that particular soft-bottom animals are generally closely connected with particular types of sediments, whereas pelagic animals are not. Although complications may occur, this condition is much more likely to be recognized in fossil material. One of the possible complications is that the animals' choice of sediment may not correspond to the sedimentary geologists idea of a lithology. Indeed, this commonly appears to be what has happened when trilobites are said to be independent of facies, which is certainly not true. In the case of *Trinodus tardus*, Kielan's review (1959, p. 28) shows that the species is widely distributed in Upper Ordovician mudstones (Bohemia, Poland, Bornholm, Scania, Västergötland) but absent from siltstones and sandstones (Kosov beds, *Dalmanitina* beds). It also seems to be absent from calcareous beds including reefs.

However, a connection with seaward and generally fine-grained sediments may be caused by a pelagic way of life as well as by life on fine-grained bottoms.

It is possible that the lack of known agnostid protaspids may have some significance. In serolid isopods the smallest larvae have entirely organic exoskeletons and calcium carbonate is introduced suddenly in one of the later moults (Bastida & Torti 1970). It may be that the agnostids, if planktic, were able to shorten the larval development by reducing the amount of energy and material necessary to construct the exoskeleton. A reduction of the pelagic larval phase is more common in pelagic animals than among benthic forms.

The odd agnostid hypostome found by Robison (1972a) is particularly characterized by its light construction. A lightening of the exoskeleton is certainly compatible with a pelagic life.

Unfortunately, no one of these characters prove that agnostids were either benthic or pelagic, although much speaks for a pelagic life. It may well be that different agnostids had different habitats though.

Robison (1972b) suggested that agnostids swam by flapping the cephalic and pygidial shields together, forcing a jet of water out between the shields. This is a possibility, particularly as an escape reaction.

A genal prosopon showing the pattern of digestive diverticula is not present in *Trinodus*, but, presumably the diverticula had roughly the same appearance as in reticulated agnostids (cf. Öpik 1961). It is symptomatic that the agnostid digestive diverticula are very different from the concentrated hepatopancreas of *Phacops* and "*Asteropyge*" (Stürmer & Bergström, MS). Coarse diverticula similar in overall appearance to those judged to be present in agnostids are found in arachnids, pycnogonids and branchiuran crustaceans among extant arthropods. Apparently this anatomical character is not confined to a particular systematic unit but instead present in arthropods feeding on fluids. The conclusion must be that the agnostids, or at least the reticulated agnostids, presumably ingested fluid food.

Morphologically the agnostids are as far removed from the pelagic and swimming type of crustaceans, exhibiting the caridoid facies, as possible. The agnostids, therefore, seem to be particularly poorly adapted to a free swimming life. Actually they are similar to the branchiurans not only in the development of the diverticula but in gross morphology as well, and therefore it is tempting to suggest that the two groups had a similar mode of life and manner of feeding. The flattened shape of branchiurans is obviously an adaptation to an ectoparasitic way of life and it is suggested that the shape of agnostids may be explained in the same way. The distribution of agnostids may therefore be a result of the distribution of the hosts. The nature of the host is not known.

The agnostids are generally supposed to have been blind. This may be true but there is also a possibility that they had ventral eyes. Branchiurans, which were found to share the flattened shape and the development of the diverticula with the agnostids, are unique among crustaceans in having well developed ventral eyes. If the modes of life of the two groups are so similar as suggested above, agnostids may also have had use for ventrally placed eyes. Actually the eyes are positioned quite close to the lateral border in several members of the Eodiscina, a group judged to be ancestral to the Agnostina, and it is easy to picture a transfer over the margin to the ventral side. Although this idea is highly conjectural it may be wise to remember that the agnostids are not proved to have been blind.

MORPHOLOGY AND LIFE OF *REMOPLEURIDES*

In most trilobites in the Skultorp fauna the exoskeleton is fairly heavy and suggestive of a benthic existence. However, *Remopleurides* sp. forms a notable exception to this rule. In this animal the light weight of the exoskeleton was achieved by means of an extreme shortening of the pleurae and diminishing of fixed and free cheeks. The eyes are very large and this in combination with the skeletal features, indicates a vagile life.

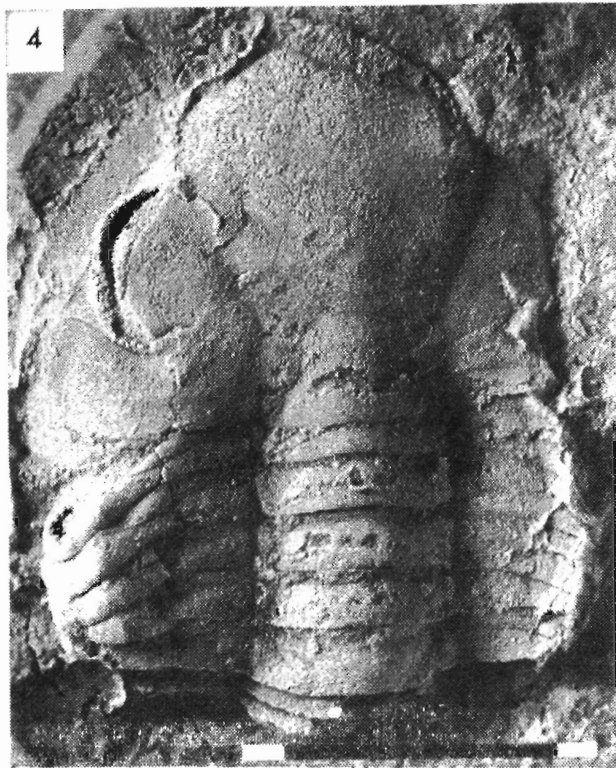
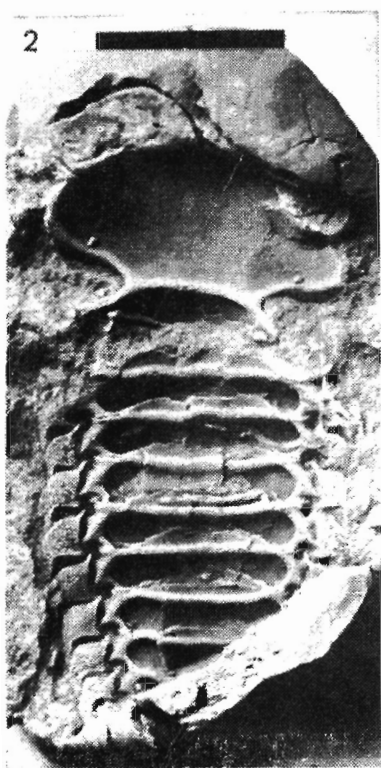
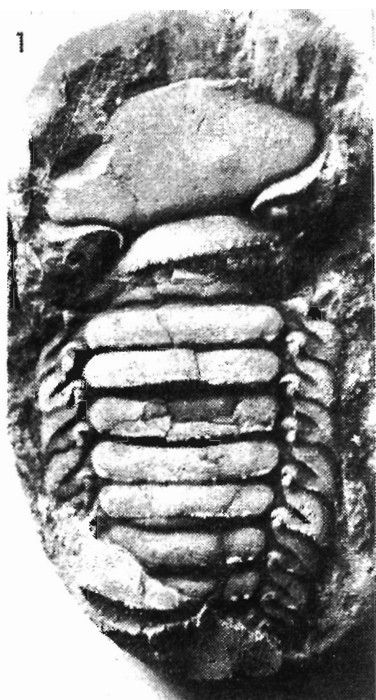
It is interesting to compare the situation with that described by Öpik (1961, pp. 40—42, 129—130) for the Cambrian trilobite *Centropleura phoenix*. As in the present case, the *Centropleura* fauna is to some degree found in thin fossiliferous bands in an otherwise poorly fossiliferous sequence, and there are dead individuals as well as exuviae, some of which are but little dismembered. The anterior pleurae of *Centropleura* were short and flat, leaving the flanks of the enrolled trilobite unprotected (this was probably not the case in *Remopleurides* sp. in spite of the short pleurae). Furthermore, in *Centropleura* the cephalon was balanced by a large pygidium and adjoining large pleurae. Öpik concludes that *Centropleura* and associated agnostids were planktic, leaving inarticulate brachiopods as the only possible benthic organisms.

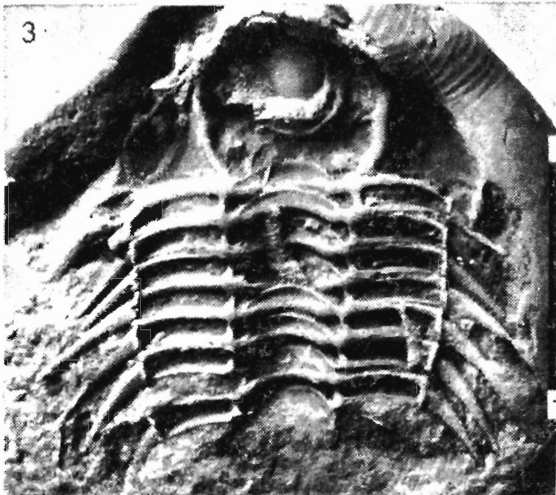
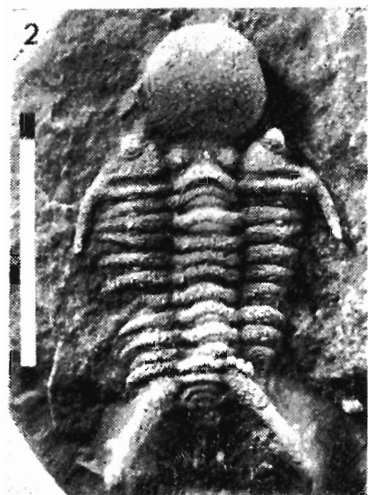
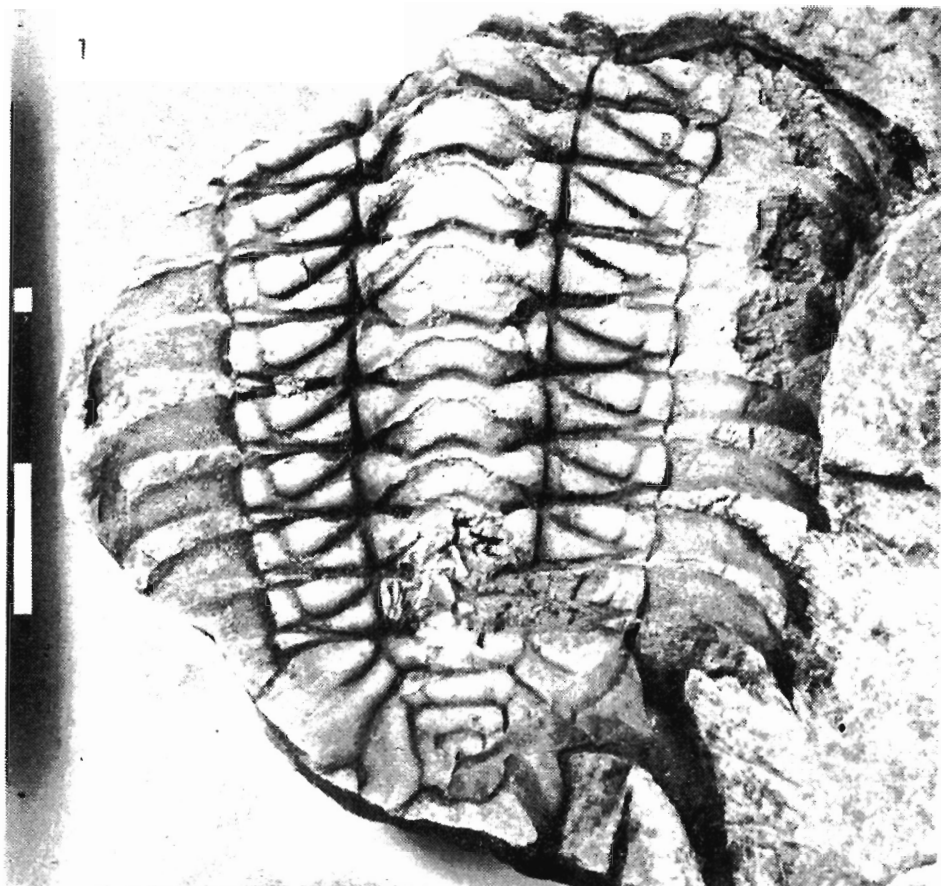
The *Centropleura* is not identical with that of *Remopleurides* sp. In the Skultorp case the bottom was certainly inhabited by a rich benthic fauna, and the fossiliferous band may perhaps be the result of increased deposition and decreased digging and bacterial activity rather than decreased deposition as suggested by Öpik for the *Centropleura* case. Nevertheless, there are certain similarities between *Centropleura* and *Remopleurides* sp., probably because both were active swimmers. In connection with the discussion of the habitat, it may also be mentioned that a Middle Ordovician remopleuridid, *Remopleurides* cf. *lata*, has been reported to occur with assumed epiplanktic brachiopods (Bergström 1968a, p. 233, Fig. 5). However, in the present case the probably increased rate of deposition and the general absence or poor representation of planktic organisms in the uppermost Ordovician beds in the area makes

PL. 1

- 1, 2 — *Remopleurides* sp.; exterior and interior view of the same individual (no. LO 4536t and 4537t).
- 3 — *Remopleurides* sp.; enrolled specimen (no. LO 4538t) with cephalic doublure well visible to the left.
- 4 — *Zetiszkella?* sp. (no. LO 4539t).

Scale in cm





it unlikely that *Remopleurides* sp. belonged to the plankton. It is tempting to regard it as belonging to nektobenthos.

It should be added that the combined presence of extremely short pleurae and enrollment capacity indicates that the exites must have been small if at all present. This may favour the idea of macroparticle feeding and possibly carnivorous habits which would be fully compatible with a nektobenthic existence.

MORPHOLOGY AND LIFE OF ILLAENIDS

In the present material illaenids (for practical reasons inclusive of *Panderia*) are not well represented, but illaenids are uniform enough in certain respects to allow some degree of generalisation.

Illaenids are characterized by a smooth vaulted test, a broad rhachis and a highly vaulted cephalon. In particular the vaulted shape and the smooth surface has induced the idea of digging habits. Thus Seilacher (1962, pp. 225—226 and Fig. 2; 1964, Fig. 2, left side; 1967, p. 74) presents the most modern view and indicates that illaenids may have been able to dig furrows in the surface (pascichnia) or tunnels (fodinichnia) in their search for food. In their digging, they would have used the shovel-shaped end of a telopodite. The shape of this is inferred from trilobite trails showing a number of parallel linear imprints (Seilacher 1962, Pl. 25, Figs 4—5). It should be added that there does not seem to be any specific reason to assign these trails to illaenids rather than to other digging trilobites.

The author agrees that the characteristics mentioned above indicate or at least allow digging habits. However, one feature in particular indicates that illaenids did not make tunnels burrowing head first. When the animal is straightened, the median line of the thorax forming a straight line, the front end of the animal is formed by the convex cranidium. It seems very unlikely that the animal dug with its appendages stretched out in front of (and morphologically dorsal to) the cephalon.

PL. 2

- 1 — *Hadromeros subulatus* (Linnarsson); the specimen preserved in the collection of the Department of Palaeontology, University of Lund (no. LO 4533t).
- 2 — *Sphaerocoryphe dentata* Angelin (no. LO 4535t).
- 3 — *Skelipyx* sp.; interior view (no. LO 4534t).

Scale in cm

Life posture. — Complete individuals, if not enrolled, are commonly preserved in a characteristic posture with the cephalon forming an angle to the thorax. This is the case with a specimen of *Illaenus crassicauda* figured by Jaanusson (1954, Pl. 1, Fig. 4). This specimen is figured so that the cephalic border is horizontal. At the same time the long axis of the eye is horizontal. According to the important results regarding trilobite eye orientation achieved by Clarkson (1966), the long axis of the eye is likely to have been horizontal in normal life posture. The idea of a connection between topological features of the eyes and life posture of the animal is strengthened by the observations of a corresponding strong connection in extant crustaceans. These conditions are excellently reviewed for anostracans, conchostracans and notostracans by Dahl (1956, pp. 139, 141, 143). The life posture of *Illaenus crassicauda* may thus have been approximately that figured by Jaanusson, with the cephalic border perhaps resting to the sediment surface and the pygidium and part of the thorax hidden below the surface. The high shape of the cephalon and the elevated eyes perhaps makes it even more probable that also the cephalon was partly embedded in the sediment.

It may be argued that the thorax and pygidium may have projected backwards instead of downwards in life. However, if the same orientation of the eye is maintained for other illaenids it is obvious that the hind part of the glabella slopes considerably downwards in many cases, and a straightening to the horizontal plane of the body behind the cephalon would imply a most remarkable curve in the dorsal line. This situation is evident even in Lower Ordovician species such as *Ottenbyaspis oriens* (Moberg & Segerberg), in which the rear end of the glabella deviates about 55° from the horizontal. In the Upper Ordovician *Panderia megalophthalma* the corresponding angle is about $55\text{--}60^\circ$ if the orientation is as indicated above and by Bruton (1968, Fig. 1B; also herein, Fig. 4).

Even more conclusive may be the report by Finch (1904) of a group of *Vogdesia vigilans* found *in situ* in the posture indicated above with thorax and pygidium projecting downwards. Although *Vogdesia* is an asaphid, it is fairly similar in its over-all shape to an illaenid and, anyway, shows that this kind of posture may have been normal in certain trilobites. I have tried to find illaenids embedded in the same position and found several in Swedish Ordovician limestones but not in the Ashgillian mudstones.

Summarizing, it appears likely that the life posture of *Panderia* and similar forms was that indicated above, with the rear part of the body tilting downwards into the sediment, and it is possible that illaenids of *Illaenus crassicauda* type had a similar posture.

Presumed illaenid trails. — If the vertical or inclined posture inferred as normal for illaenids is correct, this probably means that at least some of the trails

referred by Seilacher to illaenids were made by other animals. It is difficult to be certain, and it seems wise to take Seilacher's (1962, Pl. 25, Figs 4—5) figured trails into account. In the first of these trails there are series of apparently 7 or 8 distinct ridges (although at least 10 ridges may occur in the trail according to the explanation), which are remarkably parallel and uniform in character within each series. There seems to be a sharp longitudinal crest on each ridge. The most lateral ridges can be followed for some distance outwards, whereas the others seem to be wiped out by the neighbouring series. In the second trail there is a number of similar but less crowded series of ridges. In this case it is possible to count 6 parallel ridges in each series. There is also a number of long ridges which are said to belong to this trail but do not form distinct series.

Unfortunately no appendages are known in illaenids, but it may possibly be useful to recall what is known about appendages in other trilobites. As to the telopodites, it is difficult to imagine how this branch would have produced the parallel trails if not formed in the rather peculiar way indicated by Seilacher (1962, Fig. 2). Turning to the exites, however, there are some facts that indicate that they may have been able to produce serial trails like those figured. Thus the exites in *Phacops* (Broili 1930, Fig. 2; Pl. 22, Fig. 1), and *Cryptolithus* have a row of parallel spines which end with a bristle. As argued by Bergström (1972) exites of this type most probably in their digging activity produced bundles of parallel scratches like those described by Seilacher (1962).

If the above-mentioned trails, pictured by Seilacher, were really produced by the exites, the question of the detailed mode of formation arises. Provided that the interpretation given here is correct, there are no visible telopodite tracks in Seilacher's Pl. 25, Fig. 4. Furthermore, the distinct left and right hand tracks meet and even overlap in the midline. This indicates that the visible individual tracks were made in one end of the animal, not necessarily in the rear end (although this seems probable). The upper part of each individual track (the part which is up on the plate) is damaged by the neighbouring individual track, and the movement direction was thus upwards in the figure. The presumed exites were apparently put rather deep into the sediment immediately, and then raised successively as they moved outwards and forwards (in relation to the trail), raking the sediment. This raking action must have stirred up fine particles, which may then have been filtered in some way. Potential prey may have been caught and brought inside the exite spine curtain and within reach of the telopodites. It is probable that there was some kind of differentiation along the body, the telopodites of the fore and middle part of the body pulling forwards, whereas in the hind part, the exites were active in their raking for food and the telopodites relatively inactive.

The two pictures of trilobite life obtained from the above discussion of life position and trails are very different, and it seems improbable that the presumed illaenid trails were indeed made by illaenids. However, as the trails seem to be produced by an exite type similar to that found in such diverse groups as trinucleids, cheirurids, and phacopids, the mode of formation and the implications may still be of importance for the understanding of the trilobites treated in this paper.

Illaenid habits. — Deprived of the trail evidence, we may try to deduce something from the life posture, as this is deduced from specimens in the sediment from morphology and from similarity with *Vogdesia vigilans*. Burrowing habits must probably be combined with soft bottom habitats for illaenids. In accord with this assumption, illaenids are found in various types of clastic rocks. They are absent or rare in very fine-

-grained deposits, even if supposedly surface-dwelling trinucleids are present (cf. Hadding 1913). This may be caused by difficulties to keep the burrow open in the soft sediment. It is much more astonishing that illaenids are common in reefs (cf. Warburg 1925 and others), where soft bottom infaunal elements would not be expected to live. However, this dilemma may possibly help to explain something of the way of living and feeding in illaenids. As indicated by the probable life posture, the burrow made by the illaenids was presumably a dwelling burrow (dom-ichnion according to Seilacher 1953 and 1964) rather than a feeding burrow (fodinichnion or pascichnion of Seilacher 1953 and 1964). For making dwelling burrows in the reef, small pockets filled with sediments may be enough, and pockets with different kinds of fillings are commonly seen in many Ordovician reefs. In this environment the illaenids may have had a comparatively rich supply of food, whether they fed as predators, scavengers, or mud or suspension feeders. The common degeneration of eyes in illaenids indicates that at least many of them were not predators. However, the degeneration is not a feature common to all illaenids, and *Panderia megalophthalma*, which is known from the Skultorp fauna, has quite large lateral eyes (Fig 3). The presence of large

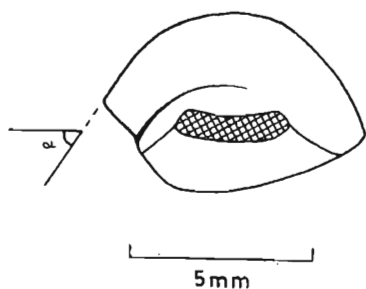


Fig. 3

Panderia megalophthalma — cephalon oriented in supposed life posture with horizontal compound eyes; the posterior part of the cephalon slopes backwards with the angle a , and the thorax must have protruded downwards in the same direction

eyes certainly does not preclude any of the three feeding methods proposed above, but at the same time it is obvious that well developed eyes are most necessary in predators and of least use in suspension feeders. Anyway, different illaenids may differ in regard to feeding methods, and one particular species like many extant crustaceans may have been able to feed in more than one way. The lack of actual information of appendage morphology makes further discussion on this point unfruitful.

MORPHOLOGY AND LIFE OF CHEIRURIDS

Cheiruridae. — Among the cheiruridids in the Skultorp fauna is *Hadromeros subulatus*, and it is interesting to find that one of the best known trilobite appendage types belong to the related *Ceraurus pleurexanthemus* (for the latest treatment and for references see Bergström 1969).

Although the appendage morphology in *H. subulatus* may have been different from that in *C. pleurexanthemus*, the latter may form the basis for a short discussion.

The exite (Størmer 1939, Figs 8—10 and Pls 5—7; 1951, Figs 8—9; Bergström 1969, Fig. 1) has a comparatively low number of spines, which radiate from a relatively narrow base. The arrangement of spines may thus have some features in common with the corresponding arrangement in *Cryptolithus* and *Phacops*. However, it is important to notice that there are also differences. Thus, in *Ceraurus* the spines, if correctly interpreted, are comparatively short, end along a curved line rather than in a straight line, and radiate from the base rather than run parallel to one another (the latter difference was pointed out for the author by Prof. Whittington). This indicates a function different from that deduced for trinucleids (*Cryptolithus*) and *Phacops*. Furthermore, the telopodite is devoid of the sharp knee and of the spines on the medial (inner) surface found in *Cryptolithus* and *Phacops*.

The picture of the mode of life and feeding in *Ceraurus* achieved in this way is mostly negative. The exites appear not to have taken any part in feeding (Bergström 1969, pp. 408—11), and the morphology of the telopodites indicates that the animal was unable to catch large prey. Also the possible absence of enditic prolongations functioning as jaws on the coxae (Størmer 1939, p. 178) suggests that no large particles could be eaten. The over-all morphology of the appendages does not indicate any specialization towards burrowing or swimming habits. It is possible that *Hadromeros* led its life mainly crawling on the bottom. The food may perhaps have been unconsolidated sediment or organic particles (decaying carcasses?) which may have been ingested directly without the aid of the appendages.

There are several possible errors in this explanation, if applied to *Hadromeros subulatus*. For instance, we do not know if the appendages of *H. subulatus* are of the same functional type as those of *C. pleurexanthemus*, and in the latter the appendages seem to be well known only in the anterior part of the thorax and the posterior part of the cephalon. Nevertheless the explanation may be considered reasonable as long as no conflicting evidence is presented.

Among the cheirurids in Skultorp are also a few cyrtometopinids belonging to the genera *Pseudosphaerexochus* and *Skelipyx*. These are among the forms with a swollen glabella. In contrast to the trinucleids with swollen glabella these genera are not confined to soft bottoms but are also found in reefs. It is tempting to suggest that these forms would have lived and fed in basically the same way in the different habitats. This is fully possible, although experience from modern seas tells that this is not always the case. Still it is reasonable to suppose that the cyrtometopids lived and fed on or above the sea floor rather than in it.

This supposition is in accord with the over-all morphology of the exoskeleton, which lacks any obvious specializations for burrowing.

The Middle Ordovician cyrtometopinid *Sphaerexochus pulcher* is one of the few trilobites, in which the hypostome has been particularly studied with regard to its orientation in relation to the length axis of the body (Whittington & Evitt 1954, pp. 89—91; Figs 25—26). In contrast to conditions in most trilobites, where the distal end of the hypostome is known to point more or less backwards, the length axis of the hypostome in *S. pulcher* is approximately perpendicular to the length axis of the body, with the distal end pointing downwards. Interestingly enough, there appears to be a correlation between feeding and the orientation of the labrum in syncaridan malacostracans. This correlation is clearly pointed out and summarized by Dahl (1956, pp. 154—156); the original observations are those of Cannon & Manton (1929) and Manton (1930). In *Paranaspides* the labrum is large and directed backwards, so that it forms a small angle with the length axis of the body. *Paranaspides* is mainly depending on its filtering apparatus for feeding, but eats also 'slime, detritus, and diatoms' covering the substrate. In *Anaspides* the labrum is also large but directed downwards with its length axis perpendicular to that of the body. This animal possesses a filtering apparatus which is not normally in use. Instead the animal eats detritus and algae and even animals such as worms and tadpoles, which are caught with the thoracopods. *Anaspides* has been observed to dig in the bottom, probably for food. *Koonunga* is a third form in this morphological series. Here the labrum is oriented as in *Anaspides* but is much smaller, with a receding distal margin. *Koonunga* has no filtering apparatus, and feeds from large food particles which are grasped by the thoracopods and brought to the mouth, where they are triturated. The same connection between morphology and function is found in other crustacean groups and by no means confined to syncarids (Dahl 1956, pp. 170—177).

The orientation of the labrum and hypostome thus appears to be strongly controlled by functional needs and may be different in closely related forms. The orientation and size in *Sphaerexochus pulcher* is closely comparable with the corresponding features in *Anaspides*, indicating a detritus or large particle food also for the former animal. This certainly tells nothing about the actual habits of the Skultorp cyrtometopinids, but on the other hand it indicates one solution which is possible within the group.

Encrinuridae. — Recently Ingham (1968, pp. 312—313, Fig. 3) suggested that *Cybeloides* was able to conceal itself in the substrate by a combination of digging and bending. In this action the diverging pygidial spines would have anchored the pygidium to the substrate when the main part of the body was dug down. While concealed in the sediment the stalked eyes would have protruded above the sediment surface. This

suggestion, based on the morphology of *C. girvanensis* and *C. loveni*, seems to be quite plausible, although the straightening force of the trilobite body would probably not have been too imposing, as inferred from the probable muscle arrangement. The main work was probably done by the appendages. In any case, the explanation is well in line with the general limitation of these *Cybeloides* species to muddy sediments. Furthermore, it is tempting to apply the suggested explanation also on other soft-bottom trilobites, including other encrinurids.

MORPHOLOGY AND LIFE OF ODONTOPLEURIDS

The ecology of *Diacanthaspis* and *Primaspis* deserves special attention. Odontopleurids are sometimes referred to as partly or wholly planktic trilobites with spines functioning as suspensive organs (cf. e.g., Richter 1919, pp. 234—238; Ruedemann 1934, p. 39; Prantl & Přibyl 1949; Whittington & Evitt 1954; for the opposite view see e.g. Clarkson 1969). However, as pointed out by Prantl & Přibyl, a planktic habit is not compatible with the general absence of odontopleurids in graptolitic shales (p. 213).

If compared with modern planktic arthropods provided with supposed suspensive spines or prolongations, i.e. crustacean zoea larvae and certain cladocerans, it is obvious that these are of a smaller size order than odontopleurids, even if the slender body of certain zoeas may reach a centimetre or more in length. Furthermore, the carbonatic exoskeleton of odontopleurids was apparently much heavier than the thin crustacean exoskeleton. The size and weight of odontopleurids as compared with the mentioned crustaceans indicate that the spines could not function effectively as suspension organs, and they were not only without much parachute effect but also hindered the animal in swimming. When compared with holoplanktic crustaceans of the same size order (*Euphausia*, *Megamycetiphanes* etc.), the odontopleurids are characterized by the development of a heavy, spiny and often tubercular exoskeleton, whereas the crustaceans have an exceedingly light skeleton without spines and ornament. In this connection it should be noticed that Whittington (1956, 1961) and Seilacher (1959) also consider spinous forms such as *Acidaspis* too large to be planktic, or at least better adapted to a benthic life. It should also be added that spines are well developed also in large odontopleurids (e.g. *Selenopeltis*, which may exceed 10 cm in length), in which a suspension function is most clearly out of discussion.

If the spines really had a suspensive function they ought to have been arranged in a fairly uniform way in relation to the centre of gravity of the trilobite body irrespective of species and size. In fact, this is not

the case. On the contrary, anterior thoracic spines of small (less than 40 mm long exclusive of spines) species may be inclined forwards by an angle of up to 25° (second thoracic segment) from the transverse line (in *Ceratocephala barrandei*; smaller angle in *C. laciniata*, *Xanionurus formosus* etc.) or backwards by an angle of up to 45° (in *Leonaspsis dormitzeri*; smaller angle in *L. lochkoviensis*, *Chlustinia keyserlingi*, *Radiaspsis radiata* etc.).

Moreover, the odontopleurid spines are not produced below a certain ventral level (Barrande 1852, Pl. 38, Fig. 6; Whittington in Moore 1959, Fig. 400b on p. O508; numerous other examples), indicating that the animal kept its ventral side toward a more or less flat surface, which may reasonably have been the bottom. Particularly noticable is the rake-like structure formed by the librigenal spines in many species. The rake has a more or less even and horizontal (or what may be supposed to be horizontal, as in Clarkson 1969, Fig. 1B) ventral (distal) delimitation. A similar rake in *Bouleia* ('Phacops') was suggested by Richter (1920, p. 41, Fig. 10) to be coupled to food-searching on soft bottoms.

Finally, it is now known that the assumption that the spines of crustacean zoeas have a suspension function is erroneous. Instead, the spines are protective and it is known that fishspawn avoid the spiny species (Thorson 1968, pp. 366—368). Thus, while the great development of spines to early palaeontologists was suggestive of a suspension function, evidence from extant planktic and benthic crustaceans, morphology, and mode of occurrence does not support this view. Among crustaceans, species with a heavy and spiny exoskeleton are characteristically benthic and defensive spines in planktic larvae are very few (in many cases only one or two) in order not to make the animal too heavy. The morphological evidence includes the fitting of the ventral side to a flat surface. The general absence of odontopleurids in graptolite shales as well as the presence of them in bioherms is further strongly contradictory to the idea of a planktic habitat.

Other features in the mode of life are more difficult to grasp. Of the two species primarily concerned in this paper, *Diacanthaspsis decacantha* seems to be mainly confined to mudstone and light-coloured shale facies as it is not known from reef or dark shale facies (Kielan 1959, p. 30; Bruton 1966, pp. 11—12). *Primaspsis* sp. is only known from a single cranidium concerned herein. However, it is apparently closely related to *P. evoluta* and may perhaps be descended from that species. *P. evoluta* and forms determined as *P. cf. evoluta* occur in a wide variety of facies from thin-cleaved black shales to mudstones and reef limestones (Bruton 1966, pp. 6—7). This is a remarkably wide ecological valence, indicating that feeding was independent of the type of subsurface. Food was apparently searched on or above the subsurface rather than beneath it.

MORPHOLOGY AND LIFE OF TRETASPIS

Tretaspis is closely allied to *Cryptolithus*, the appendages and mode of life of which were recently discussed (Bergström 1972). It is reasonable to suggest that the ventral morphology of *Tretaspis* is very similar to that of *Cryptolithus*. The sedimentary environments of the two genera are also generally similar. The discussion on *Cryptolithus* therefore may be directly applicable to *Tretaspis* and there is no reason to give an extensive repetition here.

However, the author is indebted to Prof. Leif Størmer for a valuable discussion on the exite (outer branch) of the *Cryptolithus* appendage. Størmer pointed out that the distal serrated spine was drawn somewhat too long in the figure (Bergström 1972, Fig. 2). He also questioned whether the series of exite spines is not considerably larger than suggested by the author. The latter question was caused by Beecher's illustration in Raymond (1920, Pl. 7, Figs 4—5) which shows a ventral and dorsal view of one individual. The two figures differ appreciably in the orientation of the exite spines. The cause of this difference is unknown. The exites in Raymond's Fig. 5 appear to be more proximally attached than those in Fig. 4, and are also comparatively more laterally oriented; the angle difference may exceed 30° . With this orientation the proximal spines would seem to cross the distal ones. A possible explanation is that the proximal and distal spines belong to two independent and differently oriented spine files, possibly attached to separate axial parts. All spine tips appear to reach the same general lateral level.

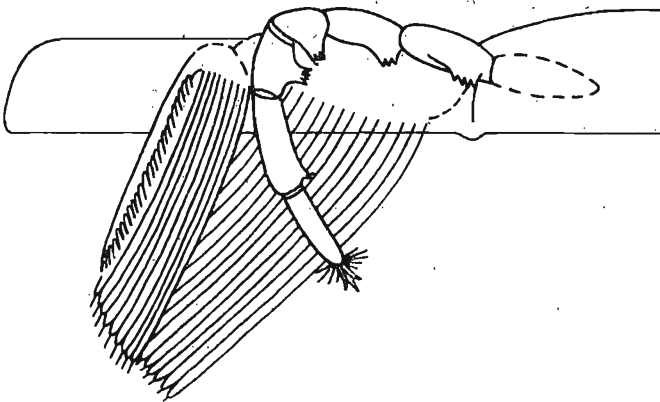


Fig. 4

Cryptolithus bellulus — ventral view of right half of thoracic segment with appendage; leg-like telopodite with distal bristle "snow-shoe" was used for walking and pushing; comb-like exite with strong spines was obviously used to rake the surficial mud but may also have had other functions (modified from Bergström, 1972)

As argued previously (Bergström 1972) the morphology of the trinucleid appendage (Fig. 4), suggests that the telopodite with its "snowshoe" of bristles pushed the animal forwards, while the exite spine tips raked the mud subsurface for food. This explanation does not exclude a swimming ability, but it is entirely unlikely that the trinucleids were pelagic.

The food of trinucleids presents a problem because we do not know the manner of ingestion. The strong glabellar furrows (and the corresponding apodemes) have been thought by several authors to indicate the presence of well developed masticatory organs. However, as summarized by Størmer (1951, pp. 132—134), the studies by Eriksson, Snodgrass, and Størmer indicate that the cephalic coxae were set well apart making a masticatory function impossible. The reconstruction of *Cryptolithus bellulus* further shows that there was no development of whole limb jaws. It is not probable that the cephalic telopodites were used for grasping small animals in the uppermost mud layer — there are no indications of any grasping specializations. However, it should not be taken for granted that the trinucleids lacked masticatory organs entirely. The author would not be surprized if the cephalic coxae were placed closer to the mid-line in life and also were provided with enditic jaws.

SIZE OF GLABELLA

It is a striking fact that in 7 species (*Tretaspis latilimba*, *T. granulata*, *Dionide* cf. *euglypta*, *Lonchodomas portlocki*, *Sphaerocoryphe dentata*, *Pseudosphaerexochus* sp., and *Skelipyx* sp.) out of 19 in the present fauna the front part of the glabella is unusually voluminous. It is interesting to compare this figure with the corresponding figure for the trilobite faunas of the Middle and Upper Ordovician Kullberg and Boda Reef Limestones in Dalarna. In that material only 12 out of 119 trilobite species had a comparable voluminous glabella (count from Warburg 1925). The author does not believe that it is reasonable to consider this difference to be caused by a mere chance. Harrington (*in* Moore 1959, pp. O99—O100) does not believe that there is a close correspondance between the size of the glabella and the size of the stomach or proventriculum because of the probability that the cephalic appendage muscles and their apodemes must have occupied most of the glabellar volume. However, this can hardly be a valid argument in the present cases of swollen glabellas. The reason for this is that the apodemes are situated either behind the swollen part of the glabella or in the posterior or extreme lateral parts of the swollen portion. Indeed, the possibility of a connection between glabellar size and development of proventriculum in *Tretaspis* was favo-

ured by Raymond (1920, p. 81), Richter (1925, pp. 168—169, Fig. 1; 1926, p. 84), and Størmer (1930, p. 107). The latter two authors even point to the possibility that impressions on the glabella in *Tretaspis bucculentus*, *T. seticornis* and *Cryptolithus tessellatus* were attachments for proventricular muscles (Richter 1926, p. 84; Størmer 1930, p. 96).

Beyrich (1846, Pl. 4, Fig. 1c) and Barrande (1852, Pl. 30, Figs 38—39) figured the trinucleid *Onnia ornata* (Sternberg) determined as *Trinucleus goldfussi* with a tubular structure extending from the rear end of pygidium into the cephalon. In the thorax and pygidium the tube is of subequal width, whereas there is a conspicuous widening beneath the glabella, particularly in front. It seems difficult to interpret this structure as anything other than the alimentary system, possibly in combination with a heart, particularly as the specimens are obviously dead individuals rather than exuviae, and also because of the very similar character of the structure in the three specimens figured. Raymond (1920, p. 81) described a fourth specimen of *Onnia ornata* which seems to corroborate the idea that the structure in question represents the alimentary canal. According to the description the structure shows the characteristics typical for the three specimens mentioned above, and in addition, part of the structure is filled with "material somewhat darker in appearance than the matrix". It seems difficult to avoid the conclusion that at least in some trinucleids the size of the glabella is in some way dependent on the development of the alimentary system either the stomach or the stomach and surrounding liver in combination.

In benthic deposit feeders and omnivores a large and muscular proventriculum may be of considerable use as a sorting and compacting organ; this is exemplified among present-day crustaceans. It is certainly suggestive that a large proportion of species with swollen glabellas occurs in a soft bottom environment while at the same time swollen glabellas are exceptional in the reef environment. Certainly the development of the hepatopancreas, which is known to surround the stomach in some phacopaceans, may also in some way be dependent on the feeding habits.

DEPTH OF WATER

There is no direct indication of the water depth at the time of sedimentation. The sediments reflect fairly calm conditions, and it is unlikely that the water was very shallow, for instance less than 20 m. On the other hand it is quite clear that the whole Baltic basin including the area in question was shelf area in Ordovician times, with comparatively slow sedimentation and moderate depth (probably as in modern shelf areas).

In an interesting paper Clarkson (1967) discusses the possibilities to use the occurrence of eye-reduction in trilobites as an indication of water depth. After a discussion of new and old evidence, Clarkson finds that there is some correlation between eye reduction and water depth although there are also different disturbing factors. These factors include sediment load in the water, latitude, and particular specializations in the arthropods concerned. In the present case there is a marked eye-reduction (7 species out of 18), but this seems to be correlated with the mode of life rather than with water depth. In two species the eyes are particularly large, but this seems also to be connected with a particular way of life. Thus, the author does not think that the development of the eyes tells much about water depth in this particular case.

Immediately after the sedimentation of the Ulunda beds, in which the fauna occurs, there was a marked shallowing of the water in the Baltic basin. In south-central Sweden this shallowing meant that the water was either very shallow (Västergötland; author's observations and measurements indicate a depth range of about 15 m within the area, and a total depth of perhaps ten or a few tens of m) or even possibly withdrawn completely (Östergötland; unpublished work by Prof. S. M. Bergström and the author). If the amount of shallowing could be estimated, it would thus be possible to get a rough idea of the Ulunda sea at Skultorp.

It is an interesting fact that the late Ordovician regression is of world-wide occurrence. This indicates that the shallowing in Västergötland was caused by a general lowering of the ocean surface rather than by local epeirogenetic movements. In the search for a cause, there is evidence of glacial deposits of possible Late Ordovician age (the author is grateful to Prof. Henno Martin of Göttingen for a discussion on this topic in 1969).

CONCLUSIONS

When trying to understand something of the ecology of the *Tretaspis* fauna it is important to note (1) that the animals had not been drifted far before burial, (2) that it was undeniably possible for at least some of them to live on the bottom, and (3) that there was a supply of organic detritus as shown by the constant presence of organic matter in the *Tretaspis* beds (cf. Henningsmoen 1948, p. 381). These points are treated below.

(1) The first point does not necessarily mean that the fauna is biocoenotic in character. One alternative would be a thanatocoenosis with pelagic and benthic constituents. There is no question about the presence of definitely benthic animals, but turning to eventually pelagic forms,

i.e. in the present fauna eventual pelagic trilobites, it is, in many cases, hard to judge with certainty if a species was pelagic or benthic. However, the sum of evidence, including absence of clear pelagic or planktic adaptations, presence of a large and heavy exoskeleton, enrolling ability, flat ventral side, morphological similarity to extant benthic species in the case of *Tretaspis*, etc., indicates that a benthic existence is the most plausible in most cases. A second alternative is that the collected fauna may form a thanatocoenosis of benthic forms. Actually, the siltstone bed is devoid of trace fossils and the presence of many dead trilobite individuals indicates that the collecting level is not a grazing ground but a graveyard. The silt must have been deposited fairly rapidly in order to embed complete animals and not disintegrated remnants. Obviously the fauna was not at home in the silty environment. The modal type of sediment in the Jonstorp and Ulunda Formation (*Tretaspis* Shale according to old terminology) is clay mudstone, and the *Tretaspis* fauna is generally intimately connected with this mudstone both geographically and geologically. It is necessary to move hundreds of kilometres to find any other lithology in the Lower and Middle Ashgillian. Therefore it seems perfectly safe to conclude that the treated fauna lived in connection with the mud of the *Tretaspis* sea and formed (part of) a biotic community (cf. Fig. 2).

(2) As to the second point, the important find of an asterozoan has already been mentioned. It is hardly possible to regard this form as anything other than a benthic animal. In this connection it should be mentioned also that a cystoid (*Sphaeronites* sp.) is known from a boulder of Upper Jonstorp Mudstone in the Gullhögen quarry, Skövde (the single specimen was collected in 1968 by Dr. Pierre Lespérance, Montréal). The presence of two species of benthic echinoderms as well as the high diversity index does not particularly support Henningsmoen's (1948, pp. 386—387) idea of a low salinity in this area at the time of deposition of the *Tretaspis* beds, at least not in the horizon in question. On the other hand, the possibility of a reduced salinity can not be totally excluded. It should be remembered that examples of extant echinoderms living in brackish waters are known, e.g. in the Baltic.

(3) Regarding the third of the above three points it is not without interest that there is a certain amount of organic matter present in the sediment. It is known from present-day oceans that detritus is extremely important for the marine nutrition economy (cf. Krey 1961; Raymond 1963, p. 502). Of suspended organic material, plankton may be more important near the surface, if importance is measured as total weight, but with increasing depth detritus dominates heavily and may reach 100%. Detritus is present at all depths and the amount is even at a depth of 10.000 m sufficiently large to serve as main food for a lot of different animals including, e.g., arthropods such as isopods and amphipods (Ray-

mont 1963, p. 543). It is further a general rule that deposit feeders dominate on soft bottoms whereas suspension feeders predominate on shell and gravel bottoms (Raymont 1963, p. 577). Doubtless suspension feeders (brachiopods) in the Ulunda Mudstone are small and unimportant in number. Thus, also for these reasons, it does not seem unreasonable with a benthic deposit feeder fauna, including many of the trilobites, in the Ulunda Formation.

The combination of different morphological, sedimentological and other features indicates that the treated fauna led a primarily benthic life in a soft-bottom environment. The determinable faunal elements point toward a dominantly epifaunal-nectobenthic character but infaunal elements were also present, as indicated by traces of digging activity below and above the trilobite horizon. When compared with present-day faunas it seems to be an unavoidable conclusion that the soft-bottom environment caused the wide distribution of successive but closely comparable *Tretaspis* faunas.

The trilobites. — The trilobites all appear to have lived close to the bottom, although they were probably all able to swim. The illaenids appear to have dug shallow burrows in which they sat with the pygidium downwards and the cephalon at least partly above the sediment surface. Nothing is known about the choice of food. They may have fed on organic matter in the sediment dug through or they may possibly have made excursions out of their burrows to catch food. Other manners are possible and there may well have been differences between different illaenids.

Tretaspis and odontopleurids have particular adaptations for a flat-lying and crawling life on the sediment surface. *Dionide* and *Lonchodomas* were probably fairly similar to *Tretaspis* in their mode of life. It is likely that *Tretaspis* searched the uppermost sediment layer for food with the aid of its exites, the spines of which may have raked the bottom. The food may have consisted of mud, enriched detritus, and small animals. Regarding the odontopleurids, nothing is known about the detailed morphology of the appendages. The distribution of many forms in diverse lithologies may indicate that they did not get their food from within the substrate. The strong spines in *Lonchodomas* and odontopleurids were for protection; they had no function in any presumed planktic floating.

The rest of the trilobites do not show any particular modifications for a life on or in the substrate. Most of them may have been fairly slow creepers and swimmers, but some may have been more mobile and referrable to the nektobenthos. As the known trilobite eyes are on the dorsal side and the mouth ventral, it is not likely that the eyes were of much use in feeding. However, there are two notable exceptions to this rule. The first one is *Remopleurides* sp., which has very large eyes direct-

ed laterally and probably with a vision field including much of the lower half-sphere. The eyes were probably used when this agile and presumably rapacious animal hunted and grasped its prey. The other exception is the species of *Cyclopyge*, in which the eyes are even larger and partly forwards and downwards directed. The prey may have consisted of unknown soft-bodied animals, ostracodes and larval trilobites. The strong exoskeleton may have prevented other trilobites from being eaten by the remopleuridid, if not very small.

Like other agnostids *Trinodus tardus* lacked dorsal eyes, but we cannot be sure that there were not ventral eyes. The development of the hepatopancreas in the agnostid trilobites is obviously very different from that of other trilobites. A similarly developed organ is found in various groups of extant arthropods living on fluid food, and it is therefore possible that the agnostids had a similar mode of feeding. Particularly striking is the comparison with the extant ectoparasitic branchiurans. These crustaceans have alimentary diverticula which in size are closely comparable with the agnostid hepatopancreas, a flattened body shape like the agnostids, and well developed eyes only on the ventral side.

Feeding methods other than filtering seems also to have been normal to other trilobites. If Størmer's observations on the cephalic appendages of *Ceraurus* are applicable also to living individuals, this cheirurid apparently lacked jaws. If this is correct the Skultorp cheirurids may have been similarly jawless. For the moment it seems unavoidable to cling to the old idea of direct ingestion of unconsolidated sediment or organic particles, but a find of cheirurid jaws would not be surprising. Cyrtometopinid cheirurids such as *Pseudosphaerexochus* and *Skelipyx* may also have fed on detritus or large particle food. This appears particularly likely in the related form *Sphaerexochus pulcher*.

Regarding the rest of the trilobites in the Skultorp *Tretaspis* fauna the evidence and indications at hand is too small to be used in an extended discussion. It may be enough to say that they probably belonged to the benthos.

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REFERENCES

- BARRANDE J. 1852. Système Silurien du centre de la Bohême, 1^{ère} Partie, Crustacés, trilobites, 1, 935 pp. Praha — Paris.
- BASTIDA R. & TORTI M. R. 1969—1970. Crustaceos isopodos: Serolidae. — Résultats scientifiques des campagnes de la Calypso, fasc. 9, 61—105. Paris.
- BERGSTRÖM J. 1968a. Some Ordovician and Silurian brachiopod assemblages. — *Lethaia* 1, 230—237. Oslo.
- 1968b. Upper Ordovician brachiopods from Västergötland, Sweden. — *Geol. et Palaeont.* 2, 1—35. Marburg/Lahn.
- 1969. Remarks on the appendages of trilobites. — *Lethaia* 2, 395—414. Oslo.
- 1972. Appendage morphology of the trilobite *Cryptolithus* and its implications. — *Ibidem*, 5, 85—94.
- BROILI F. 1930. Weitere Funde von Trilobiten mit Gliedmassen aus dem rheinischen Unterdevon. — *N. Jb. Miner. Geol. Paläont. Ser. B* 64, 293—306. Stuttgart.
- BRUTON D. L. 1966. A revision of the Swedish Ordovician Odontopleuridae (Trilobita). — *Bull. Geol. Inst. Univ. Upps.* 43, 40 pp. Uppsala.
- 1968. The trilobite genus *Panderia* from the Ordovician of Scandinavia and the Baltic areas. — *Norsk Geol. Tidsskr.* 48, 1—53. Oslo.
- CANNON H. G. & MANTON S. M. 1929. On the feeding mechanism of syncarid Crustacea. — *Trans. Roy. Soc. Edinb.* 56, 175—189. Edinburgh.
- CLARKSON E. N. K. 1966. The life attitude of the Silurian trilobite *Phacops musheni* Salter 1864. — *Scot. J. Geol.* 2, 76—83. Edinburgh.
- 1969. A functional study of the Silurian odontopleurid trilobite *Leonaspis deflexa* (Lake). — *Lethaia* 2, 329—344. Oslo.
- CRIMES T. P. 1968. *Cruziana*: A stratigraphically useful trace fossil. — *Geol. Mag.* 105, 360—364. Hertford.
- DAHL E. 1966. On the differentiation of the topography of the crustacean head. — *Acta Zool.* 37, 123—192. Stockholm.
- FINCH G. E. 1904. Notes on the position of the individuals in a group of *Nileus vigilans* found at Elgin, Iowa. — *Proc. Iowa Acad. Sci.* 1903 (11), 179—181. Des Moines.
- HADDING A. 1913. Undre dicellograptuskliffern i Skåne jämte några därmed ekvivalenta bildningar. — *Lunds Univ. Årsskr.*, N. F., Afd. 2, 9 (15), 90 pp. Lund — Leipzig.
- HENNINGSMOEN G. 1948. In: WAERN B., THORSLUND P. & HENNINGSMOEN G., Deep boring through Ordovician and Silurian strata at Kinnekulle, Västergötland. — *Bull. Geol. Inst. Univ. Upps.* 32, 374—432. Uppsala.
- INGHAM J. K. 1968. British and Swedish Ordovician species of *Cybeloides* (Trilobita). — *Scot. J. Geol.* 4, 300—316. Edinburgh.
- JAANUSSON V. 1954. Zur Morphologie und Taxonomie der Illaeniden. — *Arkiv Miner. Geol.* 1, 545—583. Stockholm.
- 1963. Classification of the Harjuan (Upper Ordovician) rocks of the mainland of Sweden. — *Geol. Fören. Stockh. Förh.* 85, 110—144. Stockholm.
- KIELAN Z. 1959. Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia. — *Palaeont. Polonica* 11, 198 pp. Warszawa.
- KREY J. 1961. Der Detritus im Meere. — *J. Cons. Int. Explor. Mer.* 26, 263—280.
- MANTON S. M. 1930. Notes on the habits and feeding mechanisms of *Anaspides* and *Paranaspides* (Crustacea, Syncarida). — *Proc. Zool. Soc. London* 1930 (3—4), 791—800 + 1079. London.
- MOORE R. C. (Ed.) 1959. Treatise on invertebrate paleontology. Part 0 (Arthropoda 1), O1—O560. Lawrence, Kansas.

- ODUM H. T., CANTLON J. E. & KORNICKER L. S. 1960. An organizational hierarchy postulate for the interpretation of species-individual distributions, species entropy, ecosystem evolution, and the meaning of a species-variety index. — *Ecology* 41, 395—399. Lancaster, Pa., & Brooklyn, N. Y.
- OPIK A. A. 1961. The geology and palaeontology of the headwaters of the Burke River, Queensland. — *Bur. Miner. Res. Geol. Geophys., Bull.* 53, 249 pp. Canberra.
- PRANTL F. & PRIBYL A. 1949. A study of the superfamily Odontopleuracea nov. superfamily (trilobites). — *Rozpr. Ústř. Úst. Geol.* 12, 221 pp. Praha.
- RAYMOND P. E. 1920. The appendages, anatomy, and relationships of trilobites. — *Mem. Conn. Acad. Arts Sci.* 7, 1—169. New Haven, Conn.
- RAYMONT J. E. G. 1963. Plankton and productivity in the oceans. 660 pp. Oxford.
- RICHTER R. 1919. Vom Bau und Leben der Trilobiten. I. Das Schwimmen. — *Senckenbergiana* 1 (6), 213—238. Frankfurt a. M.
- 1920. Vom Bau und Leben der Trilobiten. II. Der Aufenthalt auf dem Boden. Der Schutz. Die Ernährung. — *Ibidem*, 2, 23—43.
- 1925. Vom Bau und Leben der Trilobiten. III (Auszug). Die Beziehung von Glatze und Magen. — *Ibidem*, 7, 168—169.
- 1926. Vom Bau und Leben der Trilobiten. III. Die Beziehung von Glatze und Magen. — *Palaeont. Hungarica* 1, 77—89. Budapest.
- ROBISON R. A. 1972a. Hypostoma of agnostid trilobites. — *Lethaia* 5, 239—248. Oslo.
- 1972b. Mode of life of agnostid trilobites — *Int. Geol. Congr., 24th Sess., Sect. 7*, 33—40. Montreal.
- RUEDEMANN R. 1934. Paleozoic plankton of North America. — *Geol. Soc. Am., Mem.* 2, 1—141. Washington, D. C.
- SANDERS H. L. 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. — *Limn. and Oceanogr.* 5 (2), 138—153. Baltimore.
- SEILACHER A. 1953. Über die Methoden der Paläozoologie. *Studien zur Paläozoologie* 1. — *N. Jb. Geol. Paläont. Abh.* 96, 421—452. Stuttgart.
- 1959. Vom Leben der Trilobiten. — *Die Naturwissenschaften* 46, 389—393. Berlin — Göttingen.
- 1962. Form und Funktion des Trilobiten-Daktylus. — *Paläont. Zeitschr. (H. Schmidt-Festband)*, 218—227. Stuttgart.
- 1964. Biogenic sedimentary structures. In: IMBRIE J. & NEWELL N. D. (Eds.), *Approaches to paleoecology*, 296—316. New York, N. Y.
- 1967. Fossil behavior. — *Sci. Am.* 217 (2), Aug. 1967, 72—80. New York, N. Y.
- SKOGLUND R. 1963. Uppermost Viruan and Lower Harjuan (Ordovician) stratigraphy of Västergötland and Lower Harjuan graptolite faunas of central Sweden. — *Bull. Geol. Inst. Univ. Upps.* 42, 1—55. Uppsala.
- STØRMER L. 1930. Scandinavian Trinucleidae with special references to Norwegian species and varieties. — *Skr. Vidensk.-Akad. Oslo, I. Mat.-Naturv. Kl.* 4, 1—111. Oslo.
- 1939. Studies on trilobite morphology, Part 1. The thoracic appendages and their phylogenetic significance. — *Norsk Geol. Tidsskr.* 19, 143—273. Oslo.
- 1951. Studies on trilobite morphology, Part III. The ventral cephalic structures with remarks on the zoological position of the trilobites. — *Ibidem*, 29, 108—158.
- STÜRMER W. & BERGSTRÖM J. (MS). New discoveries on trilobites by X-rays (in preparation).
- THORSON G. 1968. Infaunaen, den jaevne havbunds dyresamfund. Epifaunaen: dyrelivet på vegetation, på sten, klipper, skaller, bolvaerker m.m. In: NØRRE-VANG, A. & MEYER, T. J. (Eds.), *Danmarks Natur* 3, 82—166, 167—219. København.

- WALCOTT C. D. 1918. Appendages of trilobites. — Smithsonian Misc. Coll. 67 (4), 115—216. Washington, D. C.
- WARBURG E. 1925. The trilobites of the *Leptaena* limestone in Dalarne. — Bull. Geol. Inst. Upps. 27, 1—446. Uppsala.
- WHITTINGTON H. B. 1956. Type and other species of *Odontopleuridae* (Trilobita). — J. Paleont. 30, 504—520. Tulsa, Okla.
- 1961. A natural history of trilobites. — Nat. Hist. 70 (7), 8—17. New York, N. Y.
- 1966. Phylogeny and distribution of Ordovician trilobites. — J. Paleont. 40, 696—737. Tulsa, Okla.
- & EVITT, W. R. 1954. Silicified Middle Ordovician trilobites. — Geol. Soc. Am., Mem. 59, 137 pp. New York, N. Y.
- ZIEGLER A. M., COCKS L. R. M. & BAMBACH R. K. 1968. The composition and structure of Lower Silurian marine communities. — *Lethaia* 1, 1—27. Oslo.

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ANALIZA EKOLOGICZNA ORDOWICKICH FAUN Z *TRETASPIS*

(Streszczenie)

Przedmiotem pracy jest analiza ekologiczna *tzw.* faun z *Tretaspis* charakterystycznych dla górnego ordowiku (aszgilu) środkowej, północnej i zachodniej Europy, w tym także Polski (por. Kielan 1959). Na przykładzie takiej fauny z profilu Skultorp w Västergötland w środkowej Szwecji rozpatrzono autekologię poszczególnych składników tej fauny (por. fig. 1—4, tab. 1—2 oraz pl. 1—2) wykazując, że spośród trylobitów odontopleuridy i *Tretaspis* operowały głównie na dnie, wykazując przystosowanie do płytkiego rozgrzebywania osadu i odżywiania się ofiarami o miękkim ciele; *Panderia* mogła zapewne całkowicie zagrzebywać się w osadzie, zaś *Remopleurides* i *Cyclopyge* były przypuszczalnie ruchliwymi drapieżcami, pędzącymi tryb życia nekto-bentoniczny lub nawet pelagiczny. Cechy anatomiczne agnostidów wskazują z kolei, że trylobity te, włączając także *Trinodus*, były formami pasożytniczymi. Na podstawie analizy całego zespołu organicznego i wykazywanych przystosowań szacować można, że środowisko życia rozważanych zespołów z *Tretaspis* znajdowało się w partiach basenów o głębokości rzędu 100 metrów.

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